Notes on Atlantic and other Asteroidea. 5. Echinasteridae

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Introduction

In the course of reviewing the asteroids of the Atlantic, deciding on the best subdivision of the taxonomically difficult family Echinasteridae has posed numerous problems. Echinasterids are very variable and tend to diversity into local forms, some of them sufficiently well marked and constant to be worthy of recognition as named taxa. Instances of this are provided by Fisher (1911), Hayashi (1940) and Dyakonov (1950) when dealing with the asteroids of three overlapping areas: the whole North Pacific, the vicinity of Japan and the USSR. The three of them described respectively: 8 species and 5 subspecies, of which 9 were new, 17 species of which 10 were new and 19 species with 8 new, all in the genus *Henricia*. With regard to the various Atlantic taxa, Dr F. Jensenius Madsen (pers. comm.) has recently undertaken a revision of the genus *Henricia* in connection with the series 'Marine Invertebrates of Scandinavia' but this still leaves *Echinaster*, which is well represented in the western tropical Atlantic, to be reassessed.

The present study is based partly on examination of the relevant types and partly on a large collection from the *Pillsbury, Gerda, Oregon* and other vessels. The taxa of *Echinaster (Othilia)* are the main concern, especially two new species now described, but one new species of *Henricia* is also distinguished. Diagnoses for *Echinaster (Echinaster)* and *Echinaster (Othilia)* are given and a tabular key is provided to the Atlantic species of *Echinaster*, utilizing both old and newly recognized characters now thought to be of taxonomic significance.

Because of superficial similarities between species, it must be emphasized that few reliable conclusions can be reached about the identity of most echinasterids without first removing the skin from an arm with bleach to reveal the precise form and arrangement of the underlying skeletal plates. In the case of *Henricia*, preparations of the spinelets are also invaluable.

Systematic Account

Family ECHINASTERIDAE Verrill

Echinasteridae Verrill, 1870: 343; Fisher, 1911: 258–260; Downey, 1973: 82–83; Clark & Courtman-Stock, 1976: 88.

Only three genus-group names are involved in the Atlantic fauna, namely *Echinaster* Müller & Troschel, 1840, *Henricia* Gray, 1840 and *Othilia* Gray, 1840. The main problem is the status of *Othilia* which was revived as a distinct genus from the synonymy of *Echinaster* Müller & Troschel, 1840, by Tortonese & Downey (1977) on the basis of the presence of patches of crystal bodies (or glassy tubercles) on many of the primary plates in the type species of *Othilia, Asterias echinophora* Lamarck, 1816. Such structures have not been observed in *Asterias sepositа* Retzius, 1783, the type species of *Echinaster* (see Tortonese & Madsen, 1978). Unfortunately, discovery by Clark & Tortonese (1986) that specimens from West Africa considered to be only subspecifically distinct from *E. sepositus* also have patches of crystal bodies, though ill-defined and restricted to some proximal plates, devalues this character as being of generic weight. However, there is support from two other characters which could be of generic or, at least, subgeneric weight. Firstly, the consistent enlargement to some degree of the primary carinal and adradial series of dorsolateral abactinal plates so as to frame two distinct alternating longitudinal series of skeletal meshes along the median part of each arm, coupled with further longitudinal arrangement of abradial dorso-

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laterals with transverse links between the adradials and the superomarginals. This is restricted to the species included in *Othilia*. Although *Echinaster callosus* von Marenzeller from the Indo-West Pacific has large, longitudinally arranged adradial plates, these are linked by diagonal chains of plates and the carinals are not linked in a continuous series. *E. callosus* probably merits supra-specific distinction for itself but that is beyond the scope of the present study. *E. sepositus* and the other species of *Echinaster* have an irregular reticulum of finer abactinal plates, though in some individuals the abradial plating may tend to form oblique longitudinal and short transverse lines converging on the superomarginal series. Only *E. modestus* Perrier from the west tropical Atlantic may show some enlarged adradial meshes on the proximal half of the arm suggesting the condition found in the species of *Othilia*. Secondly, there is a complete absence of actinal plates in all the species of *Othilia,* the inferomarginals bordering directly on the adambulacrals. (A superficial appearance of supposed actinal spines in some individuals is due to development of isolated spines on either the adradial ends of inferomarginals or the abradial ends of adambulacrals.) In *E. sepositus* and *E. modestus* at least one partial series of actinal plates is developed proximally. However, it must be mentioned that some non-Atlantic species currently included in *Echinaster* also lack actinal plates. Pending a full review of all of these, it seems best to treat *Othilia* as a subgenus of *Echinaster*.

Among the more useful specific characters of this subgenus now recognized are some resulting from differential development of the secondary abactinal plates developed between the adradials and the superomarginals during increase in girth of the arms—namely the abradial plates (Figs 1a,b, 3A,B). In most species of *Echinaster (Othilia)* transverse series of abradial plates initially formed are subsequently linked longitudinally or obliquely by elongate plates and it is usually these that come to bear the abradial spines. However, in some cases the spines are borne preferentially on the transverse plates. Another important character is provided by the nature of the articulations between the two kinds of plates. Usually the longitudinal ones are superimposed on the transverse plates and stand out to some extent, especially medially if the area bearing the spine is swollen, but sometimes the plating is integrated so that the longitudinal plates lie between the transverse bars flush with the surface. Surprisingly, a convex madreporite proved to be consistent throughout a wide geographical range in one new species. The shape and armament of this unique plate may be significant to a lesser extent. Campbell & Turner (1984) have also utilized the regularity of the gyri as a specific character.

ECHINASTER (ECHINASTER) Müller & Troschel

Echinaster Müller & Troschel, 1840: 102; Tortonese & Downey, 1977: 829–830,
Rhopia Gray, 1840: 281.
Verrillaster Downey, 1973: 89.

TYPE SPECIES. *Asterias seposita* Retzius, 1783, by subsequent designation by Fisher, 1913 under the name of *Asterias sagena* Retzius, 1805; validation of *A. seposita* by Tortonese & Madsen, 1979.

A subgenus of *Echinaster* in which the primary abactinal skeleton is not distinct; the plating forms an irregular reticulum medially, though sometimes resolves itself abradially into oblique longitudinal and nearly transverse lines meeting the superomarginal series; few species have a marked distinction between primary and secondary plates. The armament consists of small, usually blunt, slightly spaced spines, most often 0·75–1·0 mm long, rarely exceeding 1·5 mm; these may be limited to the nodal plates. The surface of the plates is usually smooth but exceptionally the matrix of certain proximal plates shows small inconspicuous areas of well embedded crystal bodies, usually only distinguishable when denuded. The marginal plates are in fairly regular rows and more or less enlarged in comparison with the abactinal plates, though never conspicuous. Both series are mainly aligned below the ambitus or widest past of the arm but interradially the early supermarginals may be displaced upwards to some extent if the wedge of intermarginals is widened. The inferomarginals are separated from the adambulacrals proximally at least in the Atlantic species, by at least one partial series of actinal plates. Most of the adambulacral spines are aligned in an irregular line transverse to the furrow into which one or more modified spines are inset.

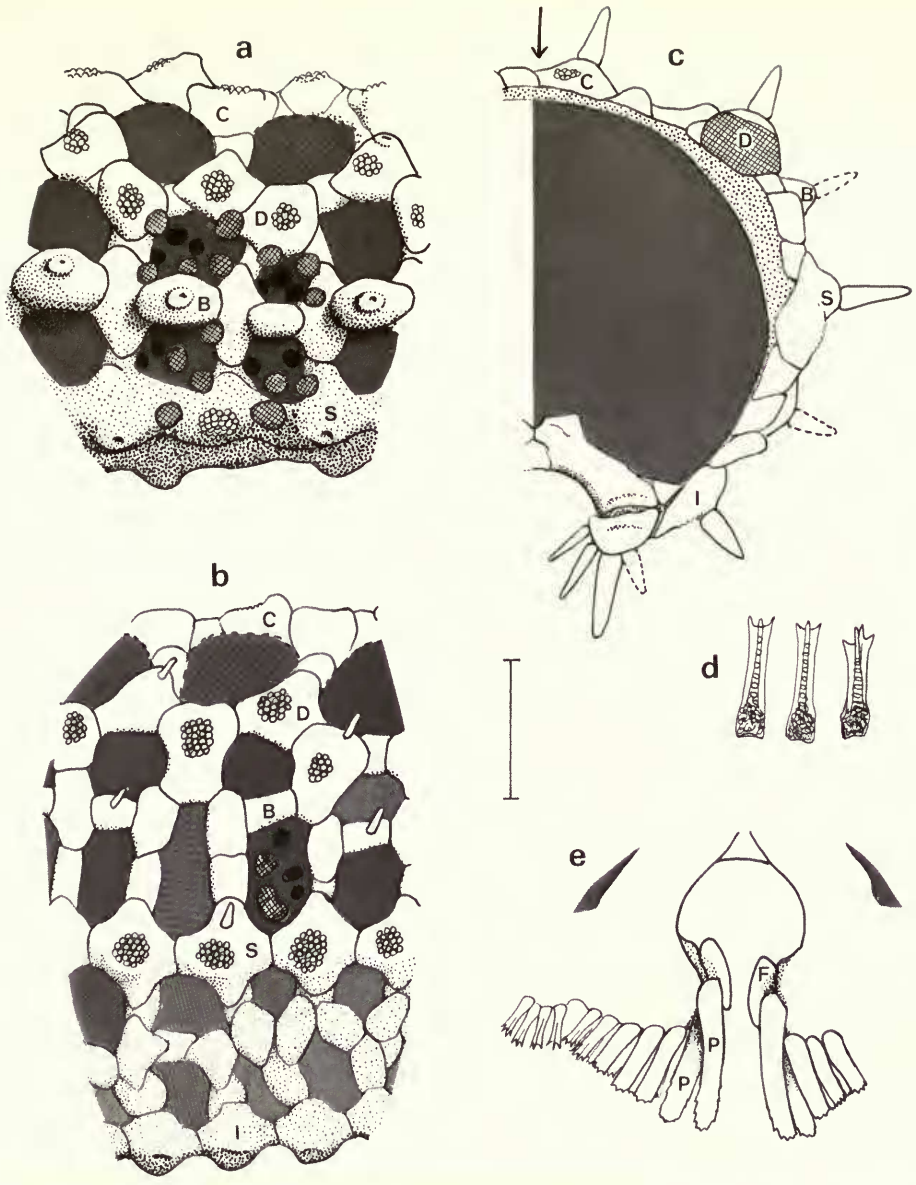

Fig. 1. a. *Echinaster (Othilia) guyanensis* sp. nov. Holotype. Lateral but slightly dorsal view of proximal part of arm (interradius to left) showing some carinal plates in profile (C), adradials (D), transverse and superimposed abradials (B) and superomarginals (S). b. *E. (O). paucispinus* sp. nov. Holotype. Lateral view, letters as in (a) with addition of inferomarginals (I). Glands (cross-hatched) and papular pores (black) shown in only a few areas. c. *E. (O.) sentus* (Say) half cross-section of proximal part of arm, plates lettered as in (a) and (b), the carinal shown offset from midline (arrowed), the adradial partly in section (cross-hatched), spines behind the plane of section shown by discontinuous lines. d,e. *Echinaster (Echinaster) downeyae* sp. nov. *Gerda* st. 311: d. abactinal spinelets, e. cross-section through furrow showing inset furrow spines (F) of two opposite adambulacral plates with a pair (P,P) of larger slightly inset spines, one behind the other, superficial adambulacral spines and also (on left only) actinal spinelets (A) of one plate, sutures omitted. The scale = 2 mm for a–c, 0·25 mm for d, 0·5 mm for e.

ECHINASTER (OTHILIA) Gray

Othilia Gray, 1840: 281; Fisher, 1911: 260 (in key), 261; Tortonese & Downey, 1977: 830.
Echinaster: Verrill, 1915: 35–36; Downey, 1973: 85–86; Walenkamp, 1976: 17–18; de Avila-Pires, 1983: 431–436.

TYPE SPECIES. *Asterias spinosa* Retzius, 1805, non Pennant, 1777, = *A. echinophora* Lamarck, 1816, by subsequent designation by Fisher, 1911.

A subgenus of *Echinaster* in which the primary abactinal skeleton is distinct or even conspicuous in adult specimens, there being a pentagon of linked primary radials and interradials on the disc around the anal area and a large pentagonal or triangular midradial skeletal mesh distal to each primary radial opposite the base of each arm; this is followed along the arm by two series of alternating adradial meshes delimited by the median longitudinal carinal series of plates with an adradial series of dorsolateral plates each side. These primary nodal plates are often linked by one or more secondary intercalary plates in adults, enlarging the meshes; other secondaries link the adradials to the superomarginals, the abradial meshes being usually smaller and subdivided by a distally incomplete longitudinal series of elongate secondary abradials; there is sometimes also a shorter second abradial series in very large specimens ($R > c.$ 60 mm) of some species, or else a longitudinal series is lacking in others where the abradial meshes are broad rectangular. The armament ranges from single large spines on some nodal primary plates, exceeding 1·5 mm in length, to smaller spaced spines or coarse spinelets on most plates including the intercalaries, sometimes multiple on some primaries; the spines of the abactinal and marginal plates form more or less regular longitudinal series totalling 7–13, most often 11. Patches of crystal bodies (glassy tubercles) are embedded in the matrix of many larger plates, especially primaries, and are visible when denuded (or dried unless the skin is very thick); the patches are occasionally reduced in extent or absent, especially when there are large single spines. The marginal plates are in regular horizontal rows, slightly enlarged, usually rhombic; the superomarginals are aligned at or just below half the height of the arm, along the ambitus or widest part of the circumference, but diverge from the inferomarginal series basally when the intermarginal plating is well developed; the inferomarginals are aligned ventrally and are contiguous with the adambulacrals throughout their extent, actinal plates being completely absent; the two inferomarginal series of adjacent rays meet interradially distal to the oral plates with usually a single interradial plate. The adambulacral spines are few and coarse, tending to be aligned in an irregular row transverse to the furrow; one or sometimes two or three spines are inset on to the furrow face of the plate, the innermost at least reduced in size, compressed and curved.

Echinaster (Othilia) guyanensis sp. nov.
Figs 1a, 2A,B

Echinaster sentus: John & Clark, 1954: 140 (listed). [Non *E. sentus* (Say, 1825)].
?*Echinaster echinophorus*: Cherbonnier, 1959: 171–172, fig. 3C,D; ?Zoppi de Roa, 1967: 281. [Non *E. echinophorus* (Lamarck, 1816)]
Echinaster brasiliensis: Downey, 1973: 88, pl. 42, figs C,D; Walenkamp, 1976: 78–81, pl. 18, figs 3,4; 1979: 72–74, pl. 15, figs 1–4, pl. 16, figs 1–4. [Non *E. brasiliensis* Müller & Troschel, 1842].

MATERIAL. *Oregon* st. 4190, 05°48′N, 52°53′W, off French Guyana (Guiana), 45 m, holotype (USNM). Also from numerous other *Oregon* and *Pillsbury* stations between Honduras and the Guyanas as well as in offshore parts of the Caribbean from Pedro Cays, S of Jamaica and from S of Haiti. The westernmost record is from the SW side of Cape Tres Puntas, Guatemala, collected by D. Nestor, via Professor T. Hopkins.

HOLOTYPE. R/r 40/9 mm = 4·4/1; Br/br (proximal breadth to distal breadth measured at 10% R from tip) 10·0/5·0 mm = 2·0/1; R/br = 8·0/1.

The five arms are fairly broad, even at the tip, somewhat tapering in the distal half, appearing rather flattened; the skin is thick enough to obscure the details of the plating but not the regular pattern; the primary pentagon on the disc is conspicuous, also the primary adradial skeletal meshes

alternating along the arms. The plate area is approximately equal to the mesh area. Some intercalary secondary plates link the nodal primaries both longitudinally and transversely. The adradials are linked to the superomarginals laterally by chains of one to three transverse plates on which are superimposed a well-developed, almost continuous, longitudinal series of elongate abradial plates, extending nearly to the tip of the arm, most of them convex medially, while 14 of those on one side of the arm which was cleaned bear an abradial spine. None of these secondary abradials bears a patch of crystal bodies (or glassy tubercles) in contrast to many of the primary carinals and adradials on which the patches usually extend for about half the exposed area of the plate. Carinal spines are fairly well developed but are reduced or absent on some nodal plates; spines are better developed on the adradials, numbering 12–14 in a longitudinal series. All these spinose primaries have the spine mounted on a rounded elevation, the larger ones inset from the distal end of the plate. The spines are single, conical, taper to a point and measure up to 1·5 mm long. The larger proximal adradial skeletal meshes include *c.* 6 papulae and 8–10 dermal glands.

The superomarginal plate series is aligned just below half the height of the arm and the plates are rhombic in shape. They number *c.* 27 on one side of the arm cleaned; of these *c.* 15 bear a single upper or median spine and have smaller patches of crystal bodies than the spineless plates which usually alternate with them. The distal spines are inconspicuous but the more proximal ones are the largest of all the spines. Intermarginal plating is restricted to the base of the arm and there are few intermarginal spines. Thus the number of longitudinal spine series on one arm is 9 rather than the more usual 11 of this subgenus, that is one carinal and two each of adradial, abradial, supero- and inferomarginals. The inferomarginal plates number *c.* 36, of which 29 have spines in one series, only sporadic plates being spineless. Actinal plates are lacking, the inferomarginals abutting directly on to the adambulacrals. Most adambulacrals bear 4 spines of which two are inset into the furrow but there may be an occasional fifth spine either at the abradial (lateral) end or slightly inset into the furrow, especially on some proximal plates. The spines form a fairly straight transverse row and are webbed together. Most of the oral plates bear 3 marginal spines and one suboral; there are probably also a few inset spines near the distal end hidden in the furrow.

The madreporite is 2·7 mm in diameter and almost circular; it is very unusual for an *Echinaster* in being distinctly convex; the fairly straight ridges which separate the gyri are studded with spinules all along their lengths.

Other specimens. The maximum R is 67 mm; R/r ranges from 4·1–4·9/1, mean 4·5/1 in 14 specimens with R > 30 mm; R/br ranges from 8·0–12·0/1, the degree of taper being rather varied and the arms narrower at the tips in some specimens. The primary skeleton is always fairly regular and conspicuous, the meshes showing dark in contrast in the dried specimens. The reticulum may be more delicate and open than in the holotype and some of the meshes may be partially confluent. The frequency of the spines and their size is often least on the carinal series but both increase towards the superomarginals. The size of the patches of crystal bodies often exceeds half the exposed area of those primary plates that bear them, the patches in the holotype being smaller than usual. The number of adambulacral spines is usually 5 on most plates of the proximal half of the arm, sometimes even 6, with 3 spines often inset into the furrow.

Discussion. Out of a total of > 150 specimens taken between Guatemala and French Guyana, only four have R > 50 mm. The distinctly convex madreporite appears to be an almost constant feature, only three specimens studied having the plate virtually flat. The body form with arms appearing slightly flattened and more tapering distally is also remarkably consistent in the material as dried. The main variations are the relative coarseness of the reticulum and the degree of development of the spines. There seems to be some local tendency in one direction or another, for instance in Venezuelan specimens the skeleton seems to be unusually delicate and the spines smaller. Further to this, the collection of the British Museum (Natural History) includes three very old specimens from Puerto Cabello, W of Caracas, Venezuela (*c.* 68°W), at least two of them collected by Brandt, the third coming via the Wyville Thomson collection and possibly also from the same source, collectors in this area of South America prior to 1850 being few. These specimens have a very delicate, almost lacelike, reticulum, a few plates in the abradial areas being longitudinally aligned and slightly superimposed; no spines or articulations for spines can be seen (though admittedly the

Table 1. Tabular key to the Atlantic species of *Echinaster (Othilia)* above and *Echinaster (Echinaster)* below the line

	1	2	3	4	5	6	7	8		9
echinophorus	20–57	3·5–4·8/4·4	c	E F	r ua	C	7(9)	SP	C	c
guyanensis	29–67	4·1–4·9/4·5	bn	O C	r u	C	9(11)	SP	I(D)(C)	n(i)
sentus	27–63	3·8–4·8/4·4	b(c)	OE F	r ux	O	11	SP	IC	n
spinulosus	35–90	4·1–5·9/5·0	ns	O F	r x	D(C)	11	S(O)B(P)	D	i
graminicola	15–27	3·3	b=c	O F	i p	C	9(11)	SB	D	i
serpentarius	41,48	4·8, 5·3	s(?b)	E F	i a	C*	11	MB	D	i
brasiliensis	35–66	4·5–5·3/4·8	b	O F	ri ax	C	9–11	S(M)B	I,D	n
paucispinus	38–63	4·5–5·8/5·3	n(sb)	O F	r x(u)	C	11(12)	SB	D	d(i)
sepositus	50–90	5·0–8·0/6·5	db(a)	O F	(r) p	N	X	SOB	I	n
sep. madseni	44–80	6·8, 7·1	a(n)	O F	(r) p	N	X	SO(B)	I	i
modestus	33–78	4·0–6·1/4·9	sa(c)	E F	r p	J*	X	O(S)B(P)	I	i
reticulatus	c.70	4·7, 5·0	c	O F	(r) p	N	X	S(O)P	—	i

1. Range of R in specimens examined:

2. Range and mean of R/r:

3. Shape of arms (of limited use because of variability);
   - c—short, stout, cylindrical, only slightly tapering.
   - d—digitate, relatively long and fingerlike, fairly broad at tips, br (breadth at 10%R from tip) usually 5–7 mm at R *c.* 40 mm.
   - b—broad throughout but slightly tapering, tips still fairly broad (Fig. 2A).
   - n—tapering evenly but markedly to fairly narrow tips, br 2·5–5·0 mm (Fig. 2C).
   - s—slender, tapering more basally than beyond.
   - a—long and tapering to attenuated tips.

4. Shape of madreporite:
   - O—almost circular.
   - E—distinctly elongate, interradial diameter at least 1·25 × tangential diameter.
   - C—surface convex.
   - F—surface flat or slightly concave.

5. Surface of madreporite:
   - p—with peripheral encircling spinules only.
   - a—with additional spinules near the periphery.
   - x—with extra spinules even centrally but peripheral ones larger.
   - u—with uniform spinules all over the ridges, or peripheral ones appearing smaller.
   - i—gyri irregular.
   - r—gyri radiating fairly regularly, separated by almost straight ridges.

6. Distinctness of primary pentagon outlining anal area on disc and of enlarged double series of primary adradial skeletal meshes along arms, at least in intact dried specimens.
   - C—conspicuous (Fig. 2A,C).
   - D—distinct.
   - J—the proximal adradial meshes at least on arms just distinguishable.
   - O—obscured by thick skin.
   - N—no distinct longitudinal arrangement.
   - *—pattern not or less distinct on disc than on arms.

7. Number of longitudinal series of abactinal and marginal plates or spines proximally: i.e. carinals, adradial and abradial dorsolateral, supero-, inter- and inferomarginals (multiple marginal spines counted as one; this is an odd number unless the carinal series is so zig-zag as to appear as two series).
   - X—only limited longitudinal arrangement or complete irregularity.

8. Abactinal spines: number, shape and alignment:
   - M—multiple on all or most plates.
   - O—often multiple but with rarely more than two spines on one plate.
   - S—predominantly or entirely single.
   - P—pointed.
   - B—blunt, often bullet shaped.
   - C—arising from apex of large convexity.
   - I—inset from distal end, sometimes central, convexity smaller.
   - D—arising near distal edge of plate from only a minimal elevation (spine often appressed distally in preservation).

9. Abactinal and superomarginal spines: size at R 40–50 mm, largest spines only.
   - c—conspicuous, at least 1·5 mm.
   - n—noticeable, 1·1–1·4 mm.
   - i—inconspicuous, 0·75–1·0 mm.
   - d—diminutive, *c.* 0·5 mm.

10. Crystal bodies (glassy tubercles): occurrence and patch size.
   - +/−—present or absent.
   - e—extending over at least half the exposed area of many primary plates.
   - r—restricted to compact patches less than half the plate area (Fig. 1a,b).
   - f—few and appearing deeply inset in the matrix or eroded, in very small patches.

10	11	12	13	14	15	16	17	18
+ r(c)	>(=)	U(S)	a(1)	15–27/30–65	R	o	3(4) 0 2(1)	T
+ e(r)	<=>	S	l	22–36/31–73	R	o	4,5 0 3,2	T
+ r(f)	>	M(S)	pl	24–35/47–82	E(R)	o	3(4) 0 2(1)	T(O)
+ e(r)	>	S	l	30–48/87–100	E	o	4(3) 1 1	O
+ e	>	S	l	20–23/c.73	(E)	o	2,3 0(1) 1	—
+ r	=	S	l	— —	E	o	5,4 0 2(1)	T
+ r	<	F	t(a)	22–32/61–100	E	o	5,4 0 1(2)	T
+ r	<(=)	F	lo	29–40/73–97	E	o	4(3,5) 0,1 2	T(O)
— —	>	R(O)	u	— —	R	s,m	3(2) 0 1	T
+ f	>	R	u	— —	R	s,m	3 0 1	T
— —	>	R(O)	u	— —	R(E)	m	5(4–7) 1 2(1)	(T)
— —	=?	R	u	— —	R	s	3(4) 0 1	?

11. Area of proximal primary abactinal plates relative to adradial mesh area (estimated approximately by eye).
    >—greater.
    =—equal.
    <—less.

12. Abradial dorsolateral plating:
    U—undeveloped, only short series of one or two intercalary plates linking adradials with superomarginals.
    F—more extensive, all plates nearly flush with the surface, consisting of chains of transverse rectangular plates, sometimes bifurcating, often linked by oblique or longitudinal plates set between the transverse ones, that is integrated with them, all these plates lacking patches of crystal bodies (Fig. 1B).
    S—consisting of longitudinal elongate and more or less convex spinose plates standing out from the surface, their ends being superimposed on the transverse chains, often forming continuous longitudinal series (Fig. 1a).
    M—of mixed form, some plates becoming modified into polygonal shapes with the addition of extra lobes and sometimes also developing a patch of crystal bodies or bearing a spine, though other proximal ones are elongate and superimposed while distal ones are all polygonal with crystal bodies, resembling the adradial plates.
    O—tending to form oblique linear series towards the superomarginals, sometimes forming a partial trelliswork.
    R—forming an irregular reticulum without consistent linear arrangement.

13. Abradial dorsolateral spines:
    a—absent or few, limited to arm bases.
    l—all or most on longitudinally-aligned or oblique plates.
    p—all or most on polygonal plates.
    t—all or most on transverse plates, even if oblique or longitudinal plates are present.
    o—all on transverse plates, which are the only ones present.
    u—uniformly on most abradial plates.

14. Spinose superomarginal plates: total number of plates in series and percentage with a main upper or distally middle spine at R 40–60 mm.

15. Occurrence of intermarginal plates:
    E—extending beyond half the arm length (measured laterally from interradius to arm tip).
    R—restricted to less than half the arm length.

16. Actinal plates:
    m—in multiple series proximally.
    s—in a single series, even on disc.
    o—lacking altogether, inferomarginals contiguous with adambulacrals throughout (note that isolated lower inferomarginal spines or lateral adambulacral ones may simulate actinal spines.

17. Adambulacral spines: total number on one plate; number on abradial or 'subambulacral' part of the plate; number inset into furrow and appearing smaller than the main furrow margin spine, its tip at a higher level.

18. Arrangement of adambulacral spines:
    T—in a transverse, almost straight series, though the spine following the main furrow margin spine may have its tip aligned distally.
    O—this same spine more obviously offset distally.

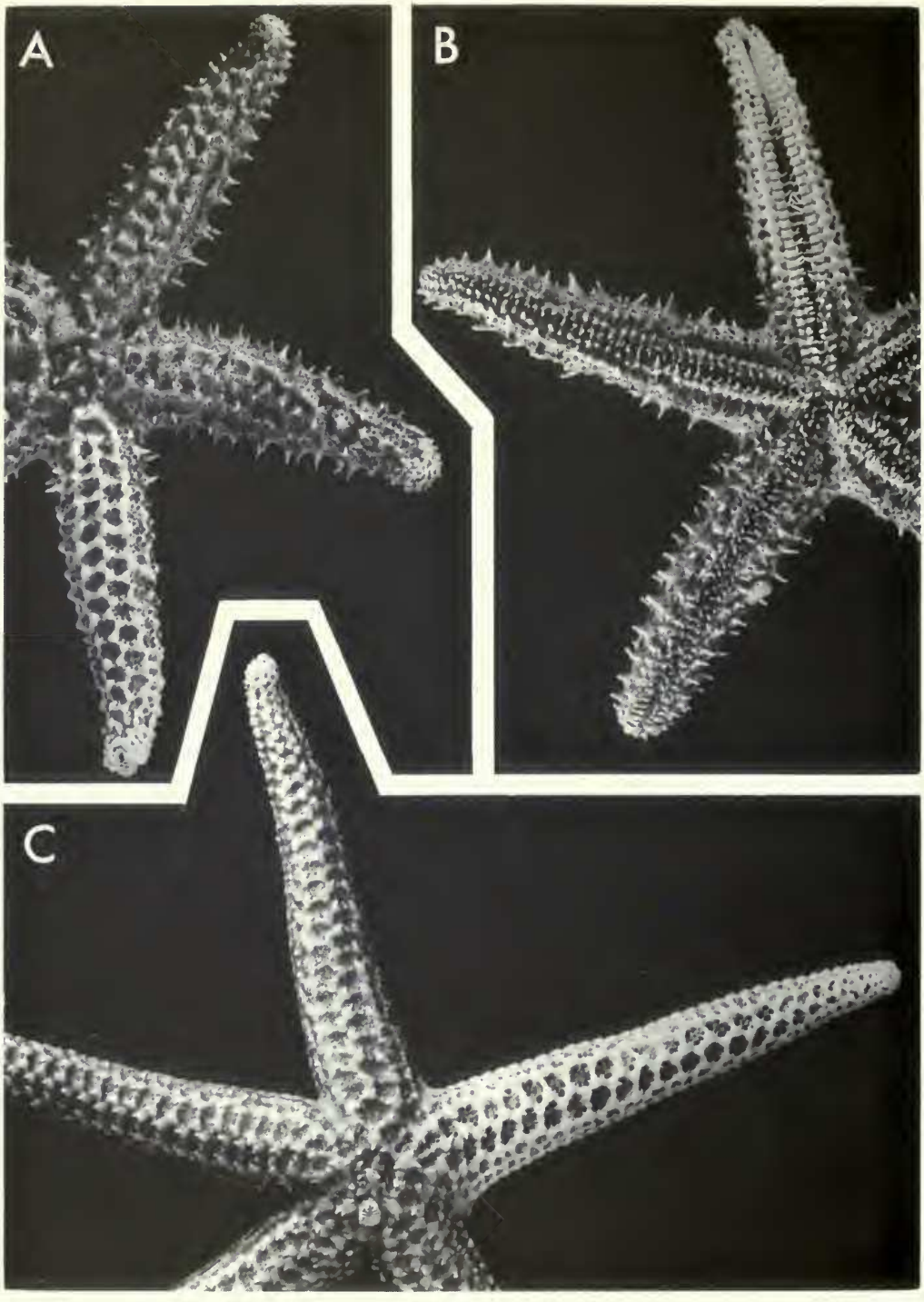

Fig. 2. A. B. *Echinaster (Othilia) guyanensis* sp. nov. *C. E. (O.) paucispinus* sp. nov. Holotypes. All × 1·5.

preservation is poor). Thomson gave his specimen an MS name derived from the last character but further material from the area is needed to establish if such an extreme variant still exists. Unfortunately, all Zoppo de Roa's Venezuelan samples (1967) appear to be from localities east of Caracas or from offshore islands to the north and east. She referred her specimens to *E. echinophorus* and described them as having prominent spines ('espinulas conspicuas') 1 + mm long in 7–9 series; they were commonly found among mangroves at 1·5 m. Surprisingly, despite abundant collections, neither Engel (1939) nor Ummels (1963) recorded any specimens of *Echinaster* from the Netherlands Antilles to the north of Venezuela.

On the northern coast of Brazil to the east of the Amazon outflow, which might form an ecological barrier, a few other specimens of *Echinaster* were taken by the *Oregon* which resemble *E. guyanensis* in some characters but are otherwise more like *E. echinophorus,* the common species on the east coast of Brazil north of *c.* 20°S. The taxonomic status of these specimens is uncertain; they will be discussed further by Clark & Downey (in prep).

The fact that such a common species of *Echinaster* with a fairly wide geographical range has previously escaped recognition can be attributed not only to the confusion as to specific limits in the genus in the tropical west Atlantic which has prevailed, but also to the superficial resemblance between *E. guyanensis* and *E. brasiliensis,* which latter species was only recently shown by de Avila Pires (1982), in a fine review of *Echinaster* in Brazil, to be limited in that country to the southern half, giving way to *E. echinophorus* in the northern part of the east coast. Due to lack of material, she was unable to establish the specific identity of any specimens from the north coast of Brazil.

RANGE. From Guatemala east and south along the Atlantic coasts of Central America and northern South America, at least to French Guyana, possibly also to westernmost north Brazil; 13–106 m; from coarse calcareous sand; shell gravel; muddy sand; sand and shells; muddy sand and gravel; or 'muddy' or 'sandy' substrates.

Echinaster (Othilia) paucispinus sp. nov.

Figs 1b, 2C, 3A,B

Thyraster serpentarius: Gray, Downey & Cerame-Vivas, 1968, fig. 29 [?non text].
Echinaster sp. B, Downey, 1973: 89, pl. 41, figs C,D.

MATERIAL. Hourglass Project st. D. 27°37′N, 83°58′W, *c.* 65 miles W of Egmont Key, Florida, 55 m, holotype (USNM), paratype (BM(NH) no. 1986.1.2.1) and second paratype (Florida Department of Natural Resources, St Petersburg Reference Collection no. I 6816). Other samples from Hourglass sts E, also W of Egmont Key, 73 m, J, K, L and M, W of Sanibel Island, 18, 37, 55 and 73 m (31 specimens). Also from St Petersburg Laboratory collection: Topsoil Bluff, Walton County, NW Florida, 30°22′N, 86°21·5′W, 12 m (2); off Panama City, NW Florida, 30°05′N, 85°46′W, (5). University of Alabama no. 8114–0157, off Panama City, *c.* 30 m; no. 8114–0147, 28°32′N, 84°19′W, *c.* 30 m; no. 8114–0153, 27°23·5′N, 84°08′W, 85 m (8). Continental Shelf Associates, Inc., via Dr R. Turner, NW of Dry Tortugas, 25°12·9′N, 83°22·7′W, 67 m (1).

HOLOTYPE. R/r 55/5·5 mm = 5·8/1; Br/br (proximal breadth to distal breadth at 10% R from tip) 10·5/4·0 = 2·7/1; R/br = 13·8/1.

The five arms are relatively slender and taper evenly to rounded tips. The skin is thin and the regular pattern of the primary skeleton conspicuous, the meshes appearing dark in dried specimens in contrast to the plates; the meshes appear about equal to the plates in total area but may slightly exceed them. Single secondary intercalary plates link most primary carinals and adradials both longitudinally and transversely on the proximal parts of the arms. The adradials are linked to the superomarginals by short transverse chains of secondary abradial plates some of which are linked longitudinally by other abradials integrated with them, that is inset on the same level, not superimposed. Most of the abradial spines are borne on these longitudinal plates. None of these secondary abradial plates bears a patch of crystal bodies (or glassy tubercles) embedded in the surface matrix, in contrast to nearly all the primary carinals and adradials. These patches are compact and relatively small, occupying less than half the surface area of the plate. This is correlated with the remarkably small size and low frequency of the spines, most of which are little more than 0·5 mm

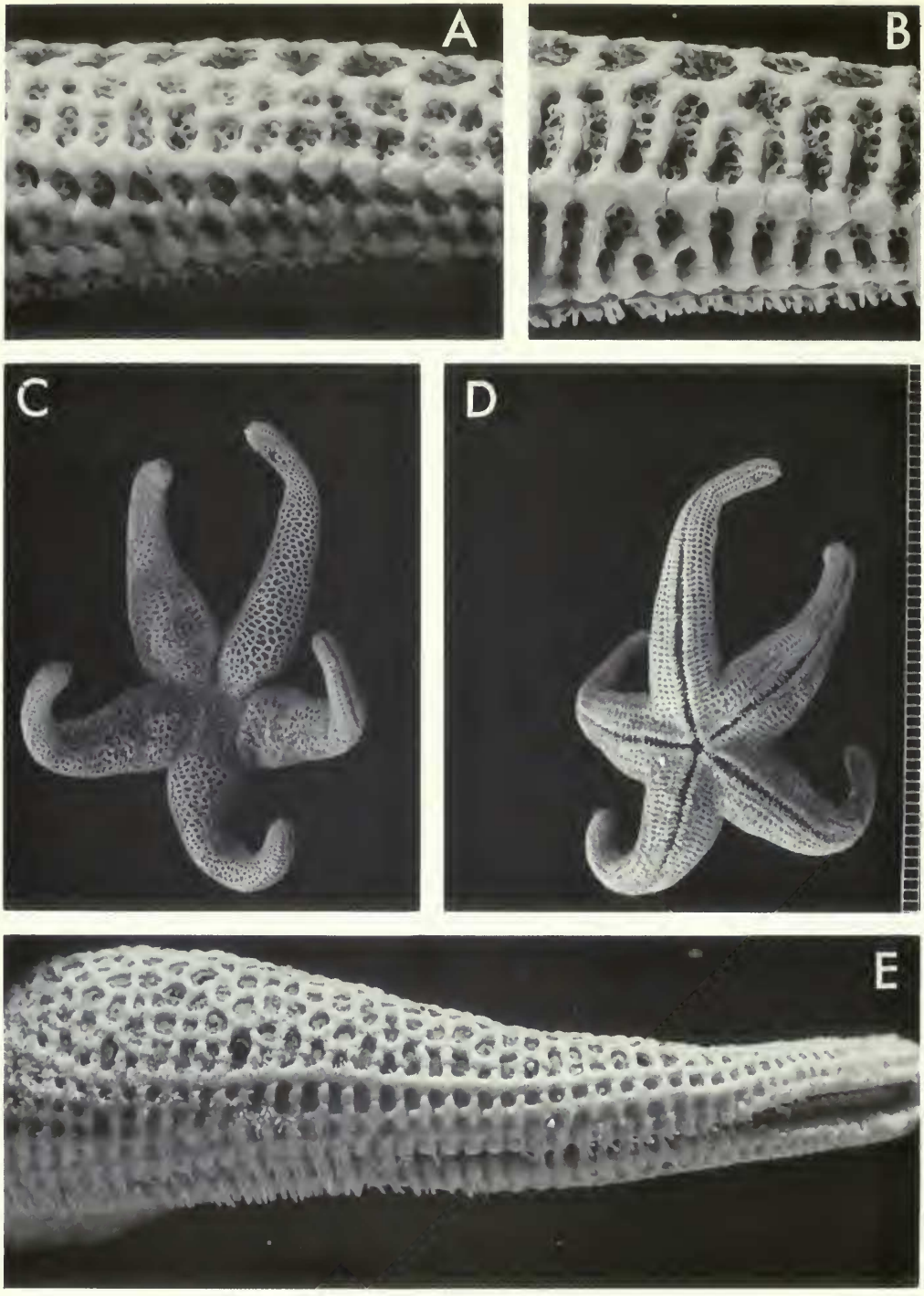

Fig. 3. A, B. *Echinaster (Othilia) paucispinus* sp. nov. Holotype (A) and paratype (B) Lateral views of proximal part of arm. C–E. *Henricia downeyae* sp. nov. Holotype. E. Lateral view of arm. A,B × 4, C,D × 1·5, E × 6.

long; however, they are rubbed and poorly preserved in this specimen; in the paratypes they are tapering and blunt-tipped but still inconspicuous, at most 0·75 mm long, and arise at the distal ends of the plates, except for those on the longitudinal abradials. The larger proximal adradial meshes include a total of *c.* 12 mixed papulae and glands in approximately equal numbers but the number of papulae declines towards the lower surface, only single glands occurring between some inferomarginals and adambulacrals.

The superomarginal plate series is aligned just below half the height of the arm. The individual plates are 4-lobed and mostly contiguous but distally some of them are slightly separated or linked by secondary plates; most bear a diminutive spine just above and distal to the patch of crystal bodies. The intermarginal plating extends for more than half the lateral arm length but is irregular, few plates bearing spines, so that there are only 9 longitudinal series of spines: one carinal and two each of adradial, abradial, supero- and inferomarginals, but all the spines are very inconspicuous. The inferomarginal plates are similar to the superomarginals in shape; on the lower side they are directly contiguous with the adambulacrals, no actinal plates being developed. The adambulacrals bear 4 or occasionally 5 spines of which two are more or less reduced in size and inset into the furrow on most plates of the proximal half of the arm; the abradial part of the plate may bear a spine when there are five but is more often bare.

The madreporite is oval, 2·7 × 2·2 mm, flat and with radiating ridges; the spinules are somewhat rubbed but there appear to be some inset from the periphery in addition to the peripheral ones. The paratype with R *c.* 59 mm probably has the armament intact and shows that spinules are absent from the central part; it has *c.* 15 peripheral spinules.

Other specimens. The paratype just mentioned also has fairly slender arms though the tips are slightly broader. It differs from the holotype mainly in lacking longitudinal abradial plates (Fig. 3B) though a few of the transverse chains of proximally three, distally two, abradials fork; the uppermost (or middle one when three) often bears an abradial spine. The plating of the wide intermarginal areas tends to follow the same pattern as that of the abradial areas and is more regular than in the holotype. Another 'Hourglass' specimen has particularly stout arms, R/r being 51–52/11·5 mm = only 4·5/1, with Br/br 13/6 mm and R/br only 8·5/1.

Discussion. This species resembles most closely *E. brasiliensis* Müller & Troschel, known from the southern half of Brazil and northern Argentina. They share reduced development of longitudinal abradial plates which are integrated, rather than superimposed, when present, coupled with the relatively slender skeletal reticulum and small size of the crystal body patches. However, in *E. brasiliensis* the abradial spines are almost invariably borne on the transverse plates, even when longitudinal or oblique ones are present and the size of these and of all the other spines is considerably greater than in *E. paucispinus*. The two are separated geographically by the ranges of *E. guyanensis* and *E. echinophorus,* the latter being the common *Echinaster (Othilia)* of the northern part of the east coast of Brazil, with sporadic records through the northern Antilles to Nicaragua, while two small specimens have just been recognized from localities in the southern Florida keys, where it overlaps with the common coral reef species *E. (Othilia) sentus* (Say).

Range. The west Florida shelf in the eastern Gulf of Mexico, NW and W of Florida, *c.* 30·5°N, 86·5°W, S to nearly 25°N; 12–85 m; associated with sponges usually in combination with coral, shell, bryozoa, algae, sand or (in one case only) rock.

Henricia downeyae sp. nov.

Figs 1d,e, 3C–E

?Henricia sp. Downey, 1973: 85, pl. 38, figs C,D.

Material. *Pillsbury* st. 1187, 18°17′N, 75°03′W, off Haiti, 1033 m, holotype (USNM). *Gerda* st. 311, 25°44′N, 79°32·5′W, off Miami, Florida, 805–787 m (2 specimens); st. 354, 25°39′N, 79°32′W, 805–832 m (4); st. 830, 25°41·5′N, 79°59′W (1). *Pillsbury* st. 689, 08°14′N, 57°38′W, off Surinam, 1370–1444 m (3). The holotype has R/r 30/7 mm = 4·3/1; Br/br (proximal to distal arm breadths, distal breadth measured at 10% R from tip) 8·0/2·5 mm = 3·2/1.

The five arms are swollen basally constricting the interradii. The abactinal reticulum is fairly open, mesh area exceeding plate area, at least when fully expanded; the plates have 2, 3 or 4 lobes and are similar in size; their contours are simply convex without well defined ridges. The spinelets of the holotype are badly rubbed and incomplete but those of the other specimens, when intact, are consistently mainly trifid with three glassy flanges ending in slightly flared points on about the same level (Fig. 1d); a few spinelets have one or two additional flanges and points; the central perforated core is narrow. The skeletal meshes of the holotype are sunken in drying but a few positive papulae, as distinct from dermal glands, are recognizable.

The superomarginal plates form conspicuous regular horizontal subambital series except interradially where those of the first 3–4 mm run obliquely upwards nearly to the ambitus. Each plate is 4-lobed but the upper lobe is shorter, making the plate appear longer than broad. The upper of the two short intermarginal series has *c.* 12 plates extending for *c.* 7 mm, the lower for only 3 mm on the arm cleaned. The intermarginal meshes are rounded, well defined and similar in shape to the abactinal meshes. The inferomarginal plates resemble the superomarginals in shape but the upper lobes are better developed giving a slightly larger average size.

The actinal plates also have 4 lobes but the adradial one is usually very short or even undeveloped. The area of each just exceeds that of the corresponding inferomarginal. The main (adradial) actinal series extends for *c.* 23 mm or about 2/3 R on the arm cleaned but the distal plates are very small. A second series of *c.* 7 plates extends for 4–8 mm proximally but is occluded interradially by the incurving of the first inferomarginal plates. Distal to the adradial series the rounded meshes or sunken areas continue to the terminal plate between the inferomarginals and the adambulacrals but the single organ in each may be a dermal gland rather than a papula.

The adambulacral plates bear numerous spines about three abreast across the abradial (subambulacral) part of the plate graduated to the several relatively coarse but not much longer spines on the furrow margin. Inset deep in the furrow is a single small spine with 2 (occasionally 3) much larger other spines on about the same level just superficial to it (see Fig. 1e), which were probably initially furrow margin spines but have become inset during growth.

The madreporite is concealed by the folding of the interradii in preservation. The best preserved of the other specimens shows a single madreporite, its irregular ridges covered with scattered spinelets not much smaller than the abactinal spinelets.

Other specimens. These too are relatively small, R up to only 25 mm, R/r 4·7–5·0/1. The best preserved, from *Gerda* st. 311, has R 19 mm; the abactinal reticulum is more compact than in the holotype, the plate and mesh areas being approximately equal; the superomarginal plate series is less distinct than that of the holotype but the inferomarginals are well developed; the intermarginal plates number only about 8 but the main actinal series extends for *c.* 12 mm (over $\frac{1}{2}$ R). There are no skeletal meshes adjacent to the adambulacrals, the only ones on the lower surface being between the inferomarginals and the actinals, but some of these appear to have papulae in them. At this small size and with the dried condition of the material the distinction between papulae and glands is not clear. Breakage of an arm shows that superficial to the deeply inset small curved furrow spine there are two larger spines arising on the same level, one proximal and one distal to it, also somewhat inset but so long that they project further than the next spines which are on the furrow margin itself (Fig. 1e). If these were initially furrow margin spines but have become inset during growth, as seems likely, it is possible that larger specimens with R > 35 mm might have additional spines inset on to the furrow face of some adambulacrals. Downey described 'about six short, stumpy spines' (presumably foreshortened as viewed ventrally) 'roughly in two vertical rows of three each' on the furrow faces of the adambulacrals of the two specimens she designated as '*Henricia* sp.', probably from the larger one, which was from the vicinity of Porto Rico and had R 62 mm. If this specimen is conspecific with the holotype of *H. downeyae,* it would support the theory of adambulacral spines shifting relative to the contours of the plates during growth. However, close scrutiny of the photographic negative of this specimen from which her plate 38C was made has shown that it has two madreporites in spite of only having five arms, while she herself found three madreporites in her smaller specimen from SW of Florida. Accordingly, both of these could be potentially fissiparous and so possibly conspecific not with *H. downeyae* but with the

fissiparous *H. sexradiata* (Perrier), which also has multiple spines inset into the furrow. In a specimen of *H. downeyae* from Surinam with the characteristic trifid spinelets, some of the adambulacral plates have two compressed curved inset furrow spines vertically one above the other and then the next two spines are almost superficial, demonstrating another variation.

AFFINITIES. Although the trifid form of the spinelets in *Henricia downeyae* agrees with that in *H. pertusa* (O. F. Müller) from the bathyal NE Atlantic, as being distinguished by Madsen (pers. comm.), that species has a more simple adambulacral armament with only a single inset spine. There is probably greater affinity with the partly sympatric West Indian *H. sexradiata* (Perrier), which shares the complex furrow armament. *H. sexradiata* differs most obviously in having six or seven arms, coupled with multiple madreporites and a fissiparous habit, also relatively more slender arms. The abactinal reticulum is probably coarser, though this character, like the occurrence of papulae on the lower side, varies in most species of the genus. The spinelets, though mainly glassy in both, have one prolonged point in *H. sexradiata,* approximating in this character to the other West Indian species *H. antillarum* (Perrier), in which the arms are consistently much more attenuated than in *H. downeyae.*

RANGE. From the Florida Strait east and south to Surinam; 342–1370 (?1444) m.

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